Sexual conflict and the mating systems of simultaneously hermaphroditic gastropods

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Abstract. Here I review the predictions, for hermaphroditic gastropods, of recent developments in mating systems and sexual conflict theory. Sexual conflict theory predicts that hermaphrodites should have a species-specific preferred sexual role. The Hermaphrodite's Dilemma model explores the consequences of this and predicts that all hermaphrodite mating systems should be based on reciprocity with cheating in a preferred role. Traditional models based on Bateman's principle predict that the male role will be preferred. Experimental and observational evidence from *Navanax inermis* (Cooper) indicate that the female role is preferred, contrary to predictions from Bateman's principle, and that the mating system is based on sperm-trading which serves to enforce reciprocation, preventing individuals from specializing in the female sexual role. Comparison of *Navanax* to other hermaphrodites suggests that the preferred sexual role is that which offers control of fertilization. This, the gamete-trading model, predicts that all hermaphroditic gastropods with sperm storage and a gametolytic gland should demonstrate a preference for the female role and a mating system based on sperm trading. This model and the Hermaphrodite's Dilemma model of strategies in a situation of sexual conflict make specific predictions about the behavior of hermaphroditic gastropods. The available literature on opisthobranchs and pulmonates suggests several interesting tests of these models but the available data are insufficient to support or refute the predictions. The mating systems of euthyneuran gastropods require investigation from the standpoint of modern mating systems theory.

Recent progress in understanding the evolution of species-typical reproductive behaviors stems largely from the analysis of mating systems in terms of a conflict of interests between the sexes (Orians, 1969; Trivers, 1972; Emlen and Oring, 1977; Parker, 1979; Hammerstein and Parker, 1987). Because such sexual conflict is assumed to be a product of the differential selective pressures associated with reproduction through sperm versus reproduction through eggs (Parker, 1979), it should exist in all anisogamous organisms (Bateman, 1948). Although work in this field (despite Ghiselin, 1974; Williams, 1975) has concentrated on a small number of taxa (largely vertebrates and insects), almost all of which have separate sexes, there has been increasing interest in the role of sexual conflict and/or sexual selection in the mating systems of a wider array of organisms, such as plants, including hermaphroditic forms (Willson and Burley, 1983; Bronstein, 1988; Galen and Rotenberry, 1988; Nakamura and Stanton, 1989) and some animals with sequential hermaphroditism (primarily fish, see Charnov, 1982, 1986; Shapiro and Boulon, 1982; Warner, 1982; Warner and Lejeune, 1985) and more recently simultaneous hermaphroditism (e.g. serranid fishes; Fischer, 1980, 1984; Fischer and Petersen, 1987; and the polychaete, *Ophyotrocha*; Berglund, 1985; Sella, 1985, 1988).

Extension of the analysis of sexual conflict to a diverse array of taxa and modes of sexuality is important for two reasons: 1) it could provide new and useful insights into the biology and evolutionary ecology of taxa of interest; 2) by examining the mating systems of a diverse array of organisms in terms of sexual conflict and/or sexual selection, we should be able to identify useful systems for testing some of the assumptions and predictions of modern mating systems theory.

The gastropods are particularly interesting in this respect because they offer: 1) a diverse array of sexual systems and reproductive strategies; 2) a variety of very complex reproductive behaviors; 3) complex genitalia, the anatomy of which is important taxonomically in many groups. Where genital anatomy is varied sufficiently to be a useful taxonomic character at the levels of genus, subgenus and species, as in some groups of gastropods (Mead, 1943; Rudman, 1974; Gilbertson, 1989; Patterson, 1989), sexual selection is likely to have been important (Eberhard, 1985). Similarly, where there are elaborate forms of courtship and copulatory behavior, and particularly where there is significant diversity within a taxonomic group, one predicts that sexual conflict and/or sexual selection has been important as a selective force.

In this paper, I 1) present predictions as to the types of sexual behavior and mating systems expected for hermaphroditic gastropods if sexual conflict is important and 2) discuss a few well-known sexual phenomena in the two predominantly hermaphroditic subclasses of gastropods (Opisthobranchia and Pulmonata) in light of predictions of

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recent models based on the assumption of sexual conflict. These two subclasses, collectively (loosely) termed the euthyneuran gastropods, are predominantly outcrossing simultaneous hermaphrodites. Hermaphroditic species offer exciting opportunities to test: 1) the hypothesis that sexual conflict exists (Leonard, 1990), because as Parker (1979) has pointed out, sexual conflict has been widely assumed but there is little evidence that it exists; 2) alternate hypotheses as to the source and nature of sexual conflict (Leonard and Lukowiak, 1991).

SEXUAL CONFLICT

SEXUAL CONFLICT AND HERMAPHRODITE MATING SYSTEMS

Sexual conflict is a conflict of interests between the two parties to a mating encounter such that one individual has more to gain (less to lose) by mating than the other does. The idea of sexual conflict is based on the common observation that among many species of animals, males are "eager" to mate with virtually any available female, to the extent of risking death and/or serious injury in fighting other males for access to females, whereas females are "coy". This phenomenon, which Darwin (1874) considered paradoxical, is usually explained by Bateman's (1948) principle, i.e. that males are more eager to fertilize eggs than females are to get their eggs fertilized because the fitness of females is limited by the resources available for egg production, whereas the fitness of males is only limited by the availability of females.

For a simultaneous hermaphrodite, sexual conflict arises if and when there is more to be gained from mating in one sexual role than in the other. In the population as a whole, reproductive success through eggs must exactly equal reproductive success through sperm (R. A. Fisher, 1958). However, the distribution of reproductive success across the population could well differ for sperm and eggs (i.e. the variances differ, see Charnov, 1979). When this is the case, there is a potential asymmetry in the pay-offs of the two sexual roles to an individual, particularly in a single encounter, and an individual's overall fitness (its reproductive success relative to the rest of the population) will depend in part on how it divides its reproductive effort (or reproductive opportunities) between the two sexual roles. That is, an individual which specializes (differs from the population average of 50:50 reproduction through sperm versus eggs) in one of the roles (that which is less costly in terms of energy expenditure, mating time, risk, etc., see below) could be able to achieve greater than average fitness. This means of course that other individuals in the population will find themselves specializing inadvertently in the more costly role, which should result in below average fitness.

Charnov (1979:2482) discussed the implications of Bateman's principle for pair-mating hermaphroditic animals, including gastropods, and recognized that, in simultaneous hermaphrodites; "There must often be a conflict of interest between mating partners — as a recipient each should be inclined to accept sperm (not necessarily for fertilization of its own eggs) in order to give its sperm away. As a donor, one should be selected to induce one's partner to use the new sperm in fertilization". He went on to suggest that both the complicated reproductive anatomy and the elaborate precopulatory behaviors of animals such as gastropods "are explicable when one realizes that the interests of the partners are often in conflict". In hermaphrodites this sexual conflict is direct, in that each individual is in direct competition with all other individuals, including its mate, for fitness. On the other hand in dioecious species sexual conflict (with the exception of conflict over parental care) is an epiphenomenon of intrasexual competition (Hammerstein and Parker, 1987).

Thus, in simultaneous hermaphrodites sexual conflict should lead to the evolution of a preference for mating in a particular sexual role, a preference that will be shared by all individuals of the species. If all individuals prefer the same role, the interests of two individuals meeting for a mating encounter will be in direct conflict. In hermaphrodites, each mating encounter could be expected to involve competition between members of the pair for the preferred role. Mating systems in hermaphrodites should reflect or represent a resolution of, this competiton for the preferred role (Leonard, 1990, unpub. data; see also below).

THE ORIGIN OF SEXUAL CONFLICT

If sexual conflict exists, the preferred sexual role will be consistent within a species, since the term implies an inherent advantage to one sexual role, but the favored role could vary between species, depending on the source of sexual conflict. Charnov based his arguments (Charnov, 1979, 1982) on the explicit assumption of Bateman's principle, i.e. that male fecundity is limited by access to eggs while female fecundity is not limited by sperm availability. While Bateman's principle is the most widely accepted explanation of sexual conflict, there are two general types of alternative explanation: mating time or rate (Baylis, 1981; Sutherland, 1986); and control of fertilization or risk (Alexander and Borgia, 1979; Leonard and Lukowiak, 1984, 1985, 1991). The first of these, the rate hypothesis, argues that a discrepancy between males and females in the minimum interval between matings, could be a source of sexual conflict. That is, if after a mating encounter, one sex (say the female) must spend a prolonged period in yolking up eggs, or some form of parental care (gestation, brooding, etc.) before being able to increase her fitness by a second mating encounter, whereas the male can inseminate many females in that same time period then one could expect the female to be "coy" and the male, "eager", even in the absence of differential energy expenditure. For a discussion of how mating rate can favor the evolution of

male parental care see Baylis (1981).

The second type of hypothesis is based on the idea that the important dichotomy between reproducing through eggs and reproducing through sperm may not be differential costs in a fixed currency (such as energy or time) but rather a differential probability that the investment that is made will pay off in the form of zygotes. If gamete production involves use of an exhaustible resource, then in economic terminology, optimal depletion of that resource (i.e. depletion which maximizes profit) must be based not only on accounting costs (the energy, time, etc. required for a particular type of reproductive act) but also the opportunity cost (that is the cost of a reproductive act now must include the value of that act if it were made at some future date, or the pay-off that could have been achieved from the other role, etc.) (Nicholson, 1978; A. C. Fisher, 1981). Alexander and Borgia (1979) suggested that an important difference between the sexes could be the extent to which control is exerted over the fate of the gametes that they produce. Alexander and Borgia (1979) argued that females, in general, produce fewer gametes not because they are limited by energy availability but rather because they invest more in ''following-up'' on that gamete, insuring that it will be fertilized. That is, one can think of females as adopting a ''risk-averse'' reproductive strategy whereas males have a ''risk-prone'' reproductive strategy. This type of model has some interesting implications for hermaphrodites.

The unique feature of hermaphrodite sexual strategies is obviously the opportunity to choose between reproduction through eggs or sperm. If, as is required for sexual conflict, the variances of these two types of strategy differ, which should be preferred, the high variance strategy or the low variance strategy? Extension of Bateman's principle to hermaphrodites (Bateman, 1948; Charnov, 1979) suggests that the male role (the high variance strategy) will be preferred (see above). However, Gillespie (1977) has demonstrated that where two genotypes yield equal average offspring number, but have unequal variances, the one with the lower variance will offer a fitness advantage. This suggests that given an opportunity to choose between a high and a low variance reproductive strategy, selection would favor the individual that opted for the low variance strategy (Leonard and Lukowiak, 1991). In Gillespie's (1977: 1012) words, ''the addition of a stochastic element to the offspring number of a genotype will effectively lower the fitness of that genotype as measured by its mean frequency in the next generation''. A practical problem in using Gillespie's principle to predict the favored sexual role for a hermaphroditic species is that we have little empirical evidence as to the relative variances of offspring production through male versus female function. In general, however, male reproductive success has been assumed to have the greater variance. Under this assumption, predictions from Gillespie's principle would be very different than those from Bateman's principle.

The gamete-trading model (Leonard and Lukowiak, 1984, 1985), developed from a comparison of the mating systems of the aglajid opisthobranch, *Navanax inermis* (Cooper) (Leonard and Lukowiak, 1984, 1985) (for discussion of the validity of the genus see Rudman, 1974; Gosliner, 1980), and a serranid fish (Fischer, 1980), is based on the premise that the preferred role for a simultaneous hermaphrodite will be the one that controls fertilization, i.e. is the last to make an irrevocable commitment of gametes. The sexual role that controls fertilization affords the greatest certainty that the investment made will result in zygotes. That is, the preferred role will have the greatest certainty of parenthood. Considered from the standpoint of selection if two reproductive options will have the same mean pay-off but one is less risky than the other, an individual with limited resources to invest will do better to play it safe (Gillespie, 1977; Philippi and Seger, 1989).

Such competing hypotheses as to the source of sexual conflict can be tested in hermaphrodites by finding species for which two of the hypotheses make opposite predictions as to the sexual role that should be favored and then determining which role is in fact preferred. For example, experimental studies designed to test the conflicting hypotheses that in *Navanax inermis*, the male role is preferred as would be expected from Bateman's principle and the egg-trading model (Fischer, 1980; see discussion in Leonard and Lukowiak, 1991), versus the conflicting hypothesis that the female role is preferred (based on the gamete-trading model), indicate a preference for the female role (Leonard and Lukowiak, 1991). In this way, the debate over the factors responsible for sexual conflict can be moved from a theoretical level to an experimental one.

DOES SEXUAL CONFLICT SHAPE MATING SYSTEMS?

The question of the importance of sexual conflict in shaping mating systems could be best answered by comparative studies. That is, we need to decide whether the mating systems observed in simultaneous hermaphrodites conform to what would be expected if sexual conflict were important. A model in the form of a game of strategy, termed Hermaphrodite's Dilemma, has been developed to analyze the situation that arises given a conflict of interest between two simultaneous hermaphrodites in a mating encounter (Leonard, 1990). This model can provide qualitative predictions as to the type of behavior and mating system to be expected under a variety of conditions.

HERMAPHRODITE'S DILEMMA

Briefly, Hermaphrodite's Dilemma is a two-person,

non-zero-sum, conditional game of strategy; the available decisions are: 1) to offer to assume both roles in a mating encounter (the cooperate decision), or 2) to mate only in the preferred sexual role and then desert without allowing the partner to mate in the preferred sexual role (the defect decision). Assuming that both players are, being simultaneous hermaphrodites, prepared to mate in both roles at all times, and that there is an advantage to mating in one role, an individual ought to be willing to assume that role in any and all encounters. Therefore, its decision in a mating encounter is not whether or not to mate in the preferred role, but whether or not it should also mate in the non-preferred role. The model predicts that the best strategy over a wide variety of conditions will be one that combines cooperating (reciprocation) most of the time, with a certain low level of defection (= cheating), which could or could not be contingent on the partner's prior behavior, depending on circumstances [i.e. w, the probability of encountering a partner again, (Axelrod and Hamilton, 1981), and whether the pay-off matrix corresponds to Prisoner's Dilemma or Chicken]. That is, given sexual conflict, the mating system of simultaneous hermaphrodites should be based on reciprocation, with cheating in a species-typical preferred sexual role occurring at a relatively low frequency, and the existence of mechanisms to reduce vulnerability to cheaters (Leonard, 1990).

Furthermore, the model suggests that mechanisms should exist to prevent cheating and/or "punish" cheaters. Although the arguments developed here should apply to all hermaphroditic gastropods, the discussion will focus on the pulmonate and opisthobranch (lumped here as "euthyneuran") gastropods because they offer a wide array of forms of (often bizarre) reproductive behavior [communal parental care (Rose and Hoegh-Guldberg, 1982), hypodermic copulation (Rivest, 1984), chain copulation (*Aplysia* and other species), and elaborate and bizarre forms of courtship (*Helix, Limax* and some other stylommatophorans)] that have been little studied. Even the familiar cases (i.e. *Helix, Limax, Aplysia*) have not been studied in light of modern mating systems theory. The analysis presented here suggests new interpretations of familiar phenomena in gastropod biology and proposes tests of important assumptions and predictions of mating system theory using comparative and experimental studies of these gastropods.

The Hermaphrodite's Dilemma model predicts that where unilateral copulation is the rule, 1) mechanisms for enforcing reciprocation exist [such mechanisms could include explicit alternation of sexual roles, such as that described for *Navanax* (Leonard and Lukowiak, 1984, 1985)], 2) effective reciprocity is achieved by random mating within a small mating group [there is some evidence to suggest that *Aplysia californica* Cooper form small, relatively stable mating clusters (Kupfermann and Carew, 1974)], or 3) willingness to copulate in the less preferred role is maintained by the con-

ditions of the Chicken matrix (Riechert and Hammerstein, 1983). For example, *Lymnaea stagnalis* (L.) are always ready to copulate as females, the preferred role according to the gamete-trading model, but become willing to copulate as males after periods of isolation (v. Duivenboden and ter Maat, 1985). Alternatively, if the mating system were not based on reciprocation, one would expect to see aggressive attempts to force copulation by individuals acting in the favored sexual role, with the victim attempting to avoid copulation and/or to retaliate by assuming the favored role, as could be the case in some leeches (Leonard, unpub. data).

The problem faced by a pair of simultaneous hermaphrodites in a mating encounter differs from that described in the classical Prisoner's Dilemma (Luce and Raiffa, 1957; Davis, 1983) or in the formal Hermaphrodite's Dilemma model (Leonard, 1990) in that a player has information about the decision made by its partner, and in general, one player will have to make the first move. One possible tactic in this situation would be the "Quick-Draw" approach; making the first move and assuming the preferred role, leaving the partner to either assume the non-preferred role or pass up the chance to mate. If the partner agreed to assume the non-preferred role, it would be possible for the initiator to either "cheat" (by leaving without reciprocating) or to reciprocate, by offering to mate in the non-preferred role also. This type of tactic could result in the evolution of either 1) "Hit-and-Run" mating encounters, such as those of some leeches (see above), or 2) insistence by the party of the second part on strong assurance that the initiator will reciprocate, before the party of the second part assumes the non-preferred sexual role. The simultaneous reciprocal copulation found in many nudibranch and stylommatophoran gastropods and clitellate annelids (earthworms and some leeches) could have evolved in this way.

In species in which mating is not (or cannot be) simultaneously reciprocal, an individual pursuing a strategy such as Tit-for-Tat should advertise its willingness to reciprocate, in order to attract potential partners or to avoid rejection by a partner that it has located. Assuming the non-preferred sexual role in the first mating would be a way of accomplishing this. For such a tactic to be successful, there would have to be some protection against "cheating" by the partner. Such tactics appear to be employed as part of a Tit-for-Tat strategy in the mating systems of certain serranid fishes (Fischer, 1980, 1984) and at least one opisthobranch gastropod, *Navanax inermis* (Leonard and Lukowiak, 1984, 1984, 1991).

EUTHYNEURAN GASTROPODS

GENERAL REPRODUCTIVE BIOLOGY
(for review see Tompa *et al.*, 1984)

All but a very few species of the euthyneuran (Sub-

classes Opisthobranchia and Pulmonata) gastropods are simultaneously hermaphroditic. Among euthyneuran groups, gonochorism is common only in the opisthobranch order Acochlidioidea (Hadfield and Switzer-Dunlap, 1984; but see Wawra, 1988). While many authors refer to protandry in these taxa, this usually means only that histological investigations show mature sperm present before eggs have matured. For example, in *Limacina*, an opisthobranch considered to be protandrous, copulation appears to be simultaneously reciprocal between mature males (Lalli and Wells, 1978; other examples in Hadfield and Switzer-Dunlap, 1984). This usage has been common in the molluscan literature since at least the end of the last century (e.g. Pelseneer, 1895). Storage of allosperm (and often autosperm) is common and individuals could receive sperm which they will later use to fertilize eggs, long before eggs have been formed in the ovotestis. True sequential hermaphroditism, in which an individual is purely a sperm donor at one stage of its life and only a sperm recipient at another, is rare, if it in fact exists, in euthyneuran snails (Geraerts and Joose, 1984; Hadfield and Switzer-Dunlap, 1984; Tompa, 1984), although it is not uncommon in the prosobranch gastropods. One must be cautious, therefore, in interpreting references to functional protandry (see discussion in Ghiselin, 1965).

Reproduction through true parthenogenesis (probably automitic) has been reported for one stylommatophoran slug (Hoffmann, 1983; see also discussion in Tompa, 1984). Although the capacity for self-fertilization is not uncommon in pulmonates, and apparently exists in a few opisthobranchs (Hadfield and Switzer-Dunlap, 1984), cross-fertilization is the rule and the vast majority of euthyneuran gastropods act as simultaneous hermaphrodites throughout their reproductive lives.

The anatomy of the reproductive system of euthyneuran gastropods can be summarized as very complex, highly diverse, and taxonomically valuable at the species level. As Eberhard (1985) pointed out, these characteristics are indicative of rapid evolution, probably as a result of sexual selection. This, in turn, suggests that these gastropods should be characterized by diverse, complex and fascinating sexual behavior and mating systems. Unfortunately, our understanding of the reproductive biology of these gastropods is very scanty. For most species only the gross anatomy of the genitalia has been described; less is known at the histological level, and there have been relatively few studies that have looked directly at the physiology of various parts of the reproductive tracts. In many cases it is difficult to imagine how the genitalia would look when everted and how the various parts would fit together during copulation (see Reeder, 1986). Also, most of the available information on sexual behavior consists of casual or anecdotal observations.

In terms of sexual behavior, euthyneuran gastropods can be divided into three groups; those in which copulation is normally simultaneously reciprocal, those in which it is unilateral, and those in which copulation is unilateral and chains of copulating individuals occur commonly. As a broad genralization, simultaneous reciprocal copulation occurs in taxonomic groups in which the penis and common genital aperture (= vaginal pore) are close together on the body, while unilateral copulation is typical of taxonomic groups in which these structures are widely separated. Speaking again very generally, one can say that simultaneous reciprocal copulation is characteristic of the stylommatophoran pulmonates (exceptions include *Stenotrema*, Webb, 1948), whereas the basommatophorans have unilateral, and sometimes chain, copulation (Geraerts and Joose, 1984; Tompa, 1984). Among the opisthobranchs, simultaneous reciprocal copulation (and/or sperm transfer) is found in most of the nudibranchs, notaspideans, saccoglossans and pteropods, whereas unilateral and/or chain copulation (or sperm transfer) is more common in cephalaspideans, anaspideans, pyramidelloideans and acochlidioideans (Hadfield and Switzer-Dunlap, 1984). True copulation is the general mode of sperm transfer in euthyneuran gastropods, but hypodermic insemination and aphallic spermatophore transfer have evolved several times among opisthobranchs (Hadfield and Switzer-Dunlap, 1984). Some land slugs deposit sperm on the tip of the partner's penis (Gerhardt, 1933; Tompa, 1984). Aphallic sperm transfer apparently occurs in some basommatophorans (Geraerts and Joose, 1984). In the nudibranch *Aeolidia* sperm are deposited on the outer surface of the female gonopore (Longley and Longley, 1984).

OPPORTUNITY FOR SPERM COMPETITION

SPERM STORAGE

Although the functions of the myriad organs of gastropod reproductive systems are poorly understood, one can say that both opisthobranchs and pulmonates typically have organs for storage of allosperm and there is some evidence that allosperm could require a period of residence in the sperm storage organ before becoming competent to fertilize eggs (Hadfield and Switzer-Dunlap, 1984). The period of residence in the sperm storage organ is uncertain for most species. Hadfield and Switzer-Dunlap (1984) reported that while some opisthobranchs show a close association between copulation and egg laying, with egg laying following copulations at a fairly predictable interval, this is not always the case. Individuals could copulate many times without spawning. One *Navanax inermis*, under laboratory conditions, copulated 24 times in the female role before laying an egg mass (Leonard and Lukowiak, 1985). The record for the number of egg masses laid between copulations is apparently still held by an *Aplysia californica* taken to Woods Hole, Massachusetts, and held in isolation by MacGinitie (1934). That individual laid eggs for more than four months and the

first 15 egg masses were fertile, demonstrating that *Aplysia* can store sperm for at least two and one-half months and that the sperm storage organ can hold enough sperm to fertilize at least 15 egg masses.

In *Navanax*, one isolated individual laid nine egg masses over the course of a month. The first five egg masses developed normally; the last four were inviable. After being allowed to copulate again (once as a female and once as a male) it laid two egg masses. The first, a small inviable one, was laid within 24 hours of copulation and a large viable egg mass was laid 24 hours later. No further eggs were laid although the individual was maintained in the laboratory for another month (Leonard, unpub. data). In one case, a *Navanax* laid a fertile egg mass after 32 days of isolation (Leonard and Lukowiak, 1985). In *Navanax* both the frequency and size of egg masses vary, and this could reflect size of the animal, food availability and/or sperm stores (Leonard, unpub. data). In isolated *Hermissenda crassicornis* (Escholtz), an aeolid nudibranch, Rutowski (1983) reported that some individuals produced as many as eight egg masses that were at least partially fertile. He reported that *Hermissenda* isolated upon collection produced an average of 3.7 $\pm$ 2.5 fertile egg masses within 24 days. He reported 20 days as the longest interval between fertile egg masses but did not indicate how long sperm can be stored after a copulation. In that study, sperm-deleted animals laid egg masses approximately three days after receiving an intromission. Another aeolid, *Phestilla melanobranchia* Bergh, can lay an average of 1.5 fertile egg masses per day for two weeks before depleting the sperm received in a single mating (Harris, 1975).

The possibility of self-fertilization complicates analysis of the relationship between egg laying and copulation in both basommatophoran and stylommatophoran pulmonates. In at least two species of the basommatophoran *Lymnaea*, egg laying begins sooner in mated than in isolated individuals (Horstmann, 1955; Boray, 1964; van Duivenboden, 1983, 1984). Horstmann (1955) established that this effect was mediated by the presence of allosperm in the gametolytic gland. However, van Duivenboden (1984) reported *Lymnaea* raised in groups laid fewer eggs than did isolated individuals.

NUMBER OF MATES

There are at least two reports of apparent monogamy in opisthobranchs. Lalli and Wells (1978: 103) concluded, from anatomical evidence, that in the pelagic pteropod *Limacina inflata* (d'Orbigny) a spermatophore is formed from the prostate gland which must be reciprocally transferred to a partner, because "all *L. inflata* of the proper size have either a well-developed prostate gland or a spermatophore received from another individual, but never both structures". Since this species is anatomically protandrous, an individual presumably mates only once in its lifetime. A different type of monogamy, involving iteroparity, has been reported from aeolid nudibranchs of the genus *Phestilla*. Rudman (1981: 408) reported that for two species from Tanzania, "At a very early stage individuals would pair with another individual of the same species and they would remain nestled together for their whole lifespan, except when egg-laying or feeding." Individual mature *Phestilla* deposit one or two egg masses per day for several weeks (Harris, 1975). However, as Hadfield and Switzer-Dunlap (1984) suggested, in most opisthobranch species individuals probably mate with a number of different individuals over their lifespan.

Tompa (1984) considered that multiple mating is probably the rule for stylommatophorans and cited evidence from *Cepaea nemoralis* (L.) (Murray, 1964) that an average brood is sired by two individuals and that 10-20 spermatophores have been found in an individual. Lind (1988) concluded that sperm competition will often occur in *Helix pomatia* L. under field conditions. Multiple paternity has also been reported for basommatophorans (Mulvey and Vrijenhoek, 1981; Monteiro *et al.*, 1984; Rudolph and Bailey, 1985). In summary, the available information, while scanty, suggests that while various types of monogamy can occur, most euthyneuran gastropods mate with several sexual partners over their lives and that there is considerable potential for sperm competition and multiple paternity of egg masses. Furthermore, the ability to store sperm for long periods of time can create special problems relative to certainty of paternity. Studies of gastropod reproductive anatomy and physiology from the standpoint of sexual selection and/or sexual conflict acting through sperm competition may shed light on both the function of gastropod reproductive tracts and the evolutionary biology and speciation of gastropods.

PREDICTIONS FROM THEORY

As stated above, the Hermaphrodite's Dilemma model predicts that the mating systems of simultaneous hermaphrodites, including gastropods should a) be based on reciprocity and b) involve a detectable level of "cheating" in a favored role. In some euthyneuran gastropods, reciprocity in the mating system is obvious and here the novel prediction is that of "cheating" in a favored role. In other groups reciprocity is not obvious or not known and thus is, in and of itself, a strong prediction of the model. A further problem is to predict which sexual role will be preferred. Bateman's principle and the egg-trading model of hermaphrodite mating systems (Charnov, 1979; Fischer, 1980; see also discussion in Leonard and Lukowiak, 1991) predict that the male role will be preferred except where the male contributes something other than sperm to the mating (i.e. parental care, a nutritional investment, etc.) which makes male parental investment larger than female parental investment. Because one cannot determine which investment is larger *a priori*, I

assume here, for the sake of simplicity, that the egg-trading model consistently predicts a preference for the male role. The gamete-trading model (Leonard and Lukowiak, 1984, 1985) predicts that where the female controls fertilization the mating system will be based on sperm trading. That is, the female role will be preferred in general in euthyneuran gastropods, and that exceptions should be found in those species that lack a gametolytic gland and/or sperm storage. Thus, for most species of euthyneuran gastropod the egg-trading model predicts a preference for the male role and the gamete-trading model predicts a preference for the female roles. Specific predictions and tests of these models are discussed below.

CASE STUDIES OF MATING SYSTEMS

NAVANAX INERMIS AND SPERM-TRADING

There has been some progress in the analysis of sexual conflict in one of the unilaterally copulating opisthobranchs, *Navanax inermis* (Leonard and Lukowiak, 1984, 1985, 1987a, 1991), which has served as the stimulus for development of the gamete-trading and Hermaphrodite's Dilemma models. The mating system of *Navanax* is based on reciprocation in that pairs of individuals actively alternate sexual roles over a series of copulations. This mating system is analogous in many respects to that of the egg-trading serranid fishes (Leonard and Lukowiak, 1984, 1985; Leonard, unpub. data), in that two individuals remain together for a series of copulations but there is no long-term pair bond. The major difference is that in serranids the male role is preferred as predicted by Bateman's principle (Fischer, 1980; Leonard, unpub. data). In *Navanax*, both qualitative observations (Leonard and Lukowiak, 1984, 1985) and experimental tests (Leonard and Lukowiak, 1991) indicate that it is female, rather than the male, sexual role that is preferred. The preference for the female sexual role in *Navanax* has been hypothesized to be a consequence of female control of fertilization (Leonard and Lukowiak, 1984, 1985, 1991).

In *Navanax*, as in most euthyneuran gastropods (Pruvot-Fol, 1961; Tompa, 1984; Geraerts and Joosse, 1984; Hadfield and Switzer-Dunlap, 1984), there is both a sperm storage organ and a gametolytic gland (Rudman, 1974), and ovulation is not tied to copulation. Consequently, sperm transferred to a partner could be "wasted" in that they could be digested rather than stored, and if stored they could or could not be used for fertilization while they (the sperm) are still viable. In the serranids, on the other hand, female courtship displays are closely tied to ovulation and the "male" has reliable information as to the onset and duration of spawning (Fischer, 1980). Therefore, the "male" has greater control over the fate of its gametes than does the "female," and this could be generally true of externally-fertilizing fishes (Alexander and Borgia, 1979). The gamete-trading model

predicts that simultaneous hermaphrodites will prefer the sexual role that offers control of fertilization (Leonard and Lukowiak, 1984, 1985, 1991). Therefore, the female role should be preferred in most euthyneuran gastropods (Leonard and Lukowiak, 1985).

The mating system of *Navanax*, termed sperm-trading, represents a mirror image of the egg-trading system. In *Navanax* a sexual encounter is initiated by an individual tracking down, courting and copulating in the male role (indicating willingness to reciprocate by starting out in the less-preferred sexual role). The available evidence suggests that males maintain intromission until the partner reciprocates (Leonard and Lukowiak, 1984, 1985, 1987a, 1991). This could serve to enforce reciprocation by preventing the partner from mating again as a female before serving as a male to its current partner. The (indirect) evidence that "cheating" occurs in *Navanax* is twofold: 1) reciprocation does not always occur, and 2) the complexity and variability of behavior observed during alternation of sexual roles suggests that cheating attempts may be occurring at this time (Leonard and Lukowiak, 1985, 1987a). In *Navanax*, sperm transfer is not directly observable and at present there is no evidence as to whether or not "subtle cheating" (Trivers, 1971) in the form of failures to transfer sperm during a copulation, or the transfer of substandard quantities of sperm, is occurring.

BIOMPHALARIA AND SPERM-SHARING

Evidence for what could represent a type of "subtle," probably even "victimless" cheating on a sperm-trading mating system, does exist in planorbid basommatophoran pulmonates of the genus *Biomphalaria*. Using genetic markers, Monteiro *et al.* (1984) demonstrated that *Biomphalaria* copulating as males sometimes transfer, to a female partner, sperm that they have received from a previous partner. That is, a snail copulating as a male may inseminate its partner with allosperm instead of, or along with, autosperm. This phenomenon appeared paradoxical at first glance because Bateman's principle can not explain how an individual would benefit by distributing someone else's sperm. The most probable functional explanation of this phenomenon is that it is a form of "cheating" in a sperm-trading mating system, serving to allow a snail to receive more sperm from a partner than it gives up (in autosperm) (Leonard and Lukowiak, 1987b; Monteiro *et al.*, 1987). This prediction was made on the basis of the gamete-trading model and analogy with *Navanax* (Leonard and Lukowiak, 1985, 1987b). This is a strong prediction because although copulation in *Biomphalaria glabrata* (Say), at least, is typically unilateral and reciprocation can occur (Brenner, 1990), the details of the mating system are as yet unknown. That is, it remains to be shown that the mating system is based on reciprocation with courtship performed by the male, and a preference for the female role, as is required for sperm-trading. Sperm-

parcelling, in which only a small quantity of sperm (too little to fill the sperm storage organ) is transferred in a single copulation, is expected to form part of sperm-trading mating systems (Leonard and Lukowiak, 1984, 1985). M.E.B. Valadares-Ribeiro has obtained evidence from studies with genetic markers of sperm-parcelling in *B. tenajophila* (pers. comm. from W. Monteiro). Sperm-parcelling has yet to be demonstrated directly for *Navanax*, although there is some evidence that a single copulation as a female does not completely replenish depleted sperm stores (Leonard, unpub. data, see also above).

OTHER MATING SYSTEMS WITH
UNILATERAL COPULATION

To date, *Navanax* is the only species for which repeated alternation of sexual roles in a copulatory bout has been described. Further investigation could show that this is not uncommon in unilaterally copulating gastropods since very little is known about the copulatory behavior of most of them. However, it is clear that repeated alternation is not characteristic of some taxa, e.g. *Lymnaea*, *Aplysia*, etc. There are three types of mating interaction that have been described for these species: single non-reciprocal copulations, a single alternation of sexual roles, and chain copulation.

LYMNAEA AND OTHER BASOMMATOPHORANS

A single alternation of sexual roles commonly occurs in the lymnaeid basommatophorans, *Lymnaea stagnalis* (L.) (Noland and Carriker, 1946; Barraud, 1957; van Duivenboden, 1984) and *Stagnicola elodes* (Say) (Rudolph, 1979a) and perhaps also in the stylommatophoran genus *Partula* (Lipton and Murray, 1979). In contrast, reciprocation does not occur commonly in the planorbid basommatophoran *Bulinus globosus* (Morelet) (Rudolph, 1979b). The mechanisms by which reciprocation is enforced (or cheating prevented) in cases of a single alternation of sexual roles have not been studied in detail. In *S. elodes* and *L. stagnalis*, male sexual behavior has been shown to be induced by copulation as a female (Rudolph, 1979a; v. Duivenboden and ter Maat, 1985) and this could also be the case in *Navanax* (Leonard and Lukowiak, 1991). In *Lymnaea*, courtship is a male behavior and individuals appear to be always willing to copulate as females (van Duivenboden and ter Maat, 1985), which suggests that the female sexual role is preferred. Also, copulatory plugs have been reported in *S. elodes* and *B. globosus* (Rudolph, 1979a, b). That of *S. elodes* probably prevents a second copulation as a female for two to three hours, while in *B. globosus* the copulatory plug is presumed to be ineffective in preventing a second copulation. It would be interesting to know more about the relationship of these plugs, apparently common in basommatophorans (Geraerts and Joosse, 1984), to the mating system.

These instances of apparently unilateral and/or single reciprocal copulations offer exciting opportunities to test the Hermaphrodite's Dilemma model, because they appear at first glance to contradict the predictions of the model. The first prediction of the model is that of reciprocity. Thus in order to be consistent with the model, the cases of unilateral copulation must actually represent part of a reciprocal interaction [which is not impossible, the single alternation of *Lymnaea stagnalis* could involve a period of hours between the two copulations during which the first male rides on the shell of the first female before she begins to reciprocate (Leonard, v. Duivenboden and ter Maat, unpub. data)] or the unilateral copulations must represent a form of "cheating" obviously derived from a reciprocal mating system. The cases of a single reciprocal copulation are also puzzling. Single reciprocal copulations would be consistent with the predictions of the Hermaphrodite's Dilemma only under Game of Chicken conditions. That is, if there is a preferred role, an individual that has taken that role in the first copulation would have no reason to remain and reciprocate by assuming the less preferred role, unless there were a shortage of other mates available. Because many of the basommatophorans, such as *Lymnaea* and *Physa*, for example, typically occur in dense populations this seems unlikely. Such population densities suggest that Prisoner's Dilemma conditions should be in operation but it is axiomatic (Axelrod and Hamilton, 1981) that under Prisoner's Dilemma, reciprocation (such as Tit-for-Tat) can only evolve where the last move of the interaction is known. Otherwise, each player would benefit by refusing to reciprocate on the last move (see Leonard, 1990). Therefore, the Hermaphrodite's Dilemma model predicts that single reciprocal copulations must involve as yet identified mechanisms for enforcing reciprocation. Specifically, where a gametolytic gland exists, it should be the case that the male is able to prevent the female from leaving before reciprocating by assuming the male role with its former partner. The egg-trading model, on the other hand, would predict that individuals should compete for opportunities to copulate as males.

CHAIN COPULATION

Chain copulation consists of a mating interaction between three or more individuals in which the individual in front acts only as a female, while each middle individual acts both as a male (to the individual in front of it) and as a female (to the individual behind it) while the last individual acts only as a male. This phenomenon has been observed in a variety of euthyneuran gastropods, particularly basommatophoran pulmonates and tectibranch opisthobranchs (see various planorbids, Precht, 1936; Duncan, 1975; Kuma, 1975; Geraerts and Joosse, 1984; Hadfield and Switzer-Dunlap, 1984; Franc, 1986). Chain (and even ring) formation appears possible in virtually all species that normally copulate unilaterally, and some that usually copulate

reciprocally (e.g. *Phyllaplysia taylori* Dall, Beeman, 1970a, b), and is particularly common under crowded laboratory conditions. In some taxa, such as *Aplysia* spp., however, chain copulation appears to occur commonly in the field, and must be regarded as a normal feature of the mating system (P. Fischer, 1869; MacGinitie and MacGinitie, 1968; Ricketts *et al.*, 1968; Kupfermann and Carew, 1974; Leonard, unpub. data). Chain copulation has also been described from laboratory observations for *Acera bullata* Müller (Legendre, 1905). Geldiay (1956) concluded that chain copulation was the rule rather than the exception for Lake District populations of the freshwater limpet, *Ancylus fluviatilis* Müller, where chains of as many as seven individuals have been observed. Wesenberg-Lund (1939) reported for *Lymnaea* that chains of three individuals were not uncommon in the field (see also Crabb, 1927; Noland and Carriker, 1946; Barraud, 1957; v. Duivenboden, 1984) and that the female will next act as male to a nearby individual. There are also reports of simultaneous reciprocal copulation in *Lymnaea* (Klotz, 1889; Crabb, 1927). In other species, chain copulation is probably largely an artifact of laboratory conditions [e.g. *Physa fontinalis* (L.) (Duncan, 1959)] and rare, if it occurs at all, in the field. For example, in *Navanax* chains and/or rings of three or four copulating individuals occur commonly in the laboratory, but are very rare in the field (Leonard and Lukowiak, 1985). Rivest (1984) described group hypodermic copulation in two species of the nudibranch *Palio*, but this appears to be the exception, the rule being simultaneously reciprocal hypodermic copulation.

The Hermaphrodite's Dilemma model predicts that chain copulation should represent an obvious derivative from a reciprocal mating system. The data available in the literature are not adequate to confirm or refute this prediction and further observations are required before we can understand chain copulation as a mating system. In *Lymnaea*, mating interactions typically involve a single alternation of sexual roles between members of a pair (Noland and Carriker, 1946; Barraud, 1957; v. Duivenboden, 1984; v. Duivenboden and ter Maat, 1985; Leonard, v. Duivenboden and ter Maat, unpub. obs.) and it could be the case that chain copulations occur under conditions of high density and could represent "cheating" on a successively reciprocal system. If so, the gamete-trading model predicts that the "cheating" will consist of females avoiding male behavior, whereas the egg-trading model would predict that individuals should compete for opportunities to copulate as males. Another possibility is that mechanisms exist for reciprocation within the chain interaction. That is, individuals in chains could remain in the chain until they have copulated equally often in both roles. Some observations in both *Lymnaea* (Wesenberg-Lund, 1939) and *Aplysia californica* (Leonard and Lukowiak, 1983; Leonard, unpub. data) suggest that, as in *Navanax* (Leonard and Lukowiak, 1987a, 1991), individuals begin to act as males

after acting as females. Also, laboratory observations indicate that chains of copulating *A. californica* can break and reform and individuals can copulate several times before mating activity ceases, with some indication that females (individuals at the front of the chain) tend to act as males to either the animal at the end of the chain or a nearby individual in the subsequent copulation (Leonard and Lukowiak, unpub. data). The data, however, are too scanty to allow us to tell whether individuals alternate sexual roles within chains. In *Aplysia*, courtship is initiated by the individual that will act as a male (Kupfermann and Carew, 1974; Leonard and Lukowiak, 1983) as is the case in *Lymnaea* and *Navanax* but there is as yet no clear evidence that the female is preferred as predicted by the gamete-trading model.

THE STRANGE CASE OF *ARIOLIMAX*: SELF-MUTILATION? HERMAPHRODITES AS "CASTRATING FEMALES"?

Another intriguing observation is the report for a stylommatophoran slug, *Ariolimax,* that "they frequently gnaw off the penis at the close of copulation," (Mead 1943: 675). A certain percentage of large individuals in *Ariolimax* appear to lack completely a penis (Heath, 1916; Mead, 1943), whereas in others it is underdeveloped (Heath, 1916). Heath (1916), having hypothesized that the penis must be lost and then regenerated in this species, collected 200 individuals in an enclosure and after several weeks was able to observe two instances of copulation. He described the courtship process and stated that copulation was unilateral and that in both cases the penis was chewed off as soon as the animals began to draw apart. He indicated that in at least one case the amputation was initiated by the female who was then joined in amputation by the "possessor of the intromittent organ concerned". Upon dissection Heath found that in two of the individuals (the females in the copulations), the amputated penis extended from the genital pore internally to the distal end of the seminal receptacle. Heath found this phenomenon understandably perplexing and offered two possible explanations: 1) that the amputated penis serves as a sperm plug; 2) that the behavior is an artifact of disturbance by the observer and has evolved as a means of rapid separation when escape is necessary. Because the amputation process took over 10 min (Heath, 1916), it seems unlikely that it is an effective defense against predators but it could serve to prevent dessication. Heath mentioned that copulation is nocturnal and that intromission had lasted several hours before the animals began to separate so it may be the case that copulations starting late in the night might create a risk of dessication in the morning sun unless there was a way of rapidly terminating them. Sexual conflict theory can add 1) the possibility that the function of the sperm plug is more to prevent the mate from acting as a female again (keep other sperm out) than to prevent loss of sperm, and/or 2) the suggestion that in these her-

maphrodites an individual that amputated the penis of its mate could increase its own reproductive success as a male by decreasing the number of effective male rivals.

The Hermaphrodite's Dilemma model would predict that this behavior, if it is not merely a defense mechanism against danger of dessication or the like, must be a means of enforcing reciprocation or "cheating" on a reciprocal mating system. For example, if as predicted by the gamete-trading model, the female role is preferred it could be the case that once an individual has accumulated enough allosperm to fill its own sperm storage organ, it could not have any "reason" to mate as a male and could amputate its own penis, leaving it as a sperm plug to prevent its mate from receiving more sperm before egg-laying, thereby insuring paternity. It is barely conceivable that an individual could be able to regenerate its penis in time to get to use it in reciprocal mating interactions in order to obtain a new load of sperm after using the previous batch. In any case, the gamete-trading model predicts that *Ariolimax* which lack a penis should remain willing to copulate as females whereas the egg-trading model would predict that, because her-maphrodites should copulate as females in order to get an opportunity to copulate as males, that an individual lacking a penis ought to be unwilling to copulate as a female. Similar-ly, if the goal of copulating as a male is getting an oppor-tunity to be female, as is predicted for euthyneuran gastropods by the gamete-trading hypothesis, then *Ariolimax* should be reluctant to act as a male to an individual that lacks a penis. The egg-trading model on the other hand predicts that an in-dividual copulating as a male should not be fussy and should accept a mate with or without a penis of its own. Therefore, both gamete-trading and egg-trading predict that individuals lacking a penis will be unlikely to be involved in copulations but the egg-trading model predicts that that will be due to "coyness" of the amputee, whereas the gamete-trading model predicts that the individual lacking a penis will be unattrac-tive or rejected as a (female) mate.

The copulation of these common banana slugs of the northwest coast of the United States seems to demand further attention. We need to know: 1) whether this amputation is a defensive response or whether it occurs as a normal part of the sexual behavior; 2) how commonly this amputation occurs; 3) who amputates the penis of whom; and 4) whether this amputation occurs after an individual's first copulation or only in older individuals who may have mated with several partners. We also need to know how often these animals copulate over their life-span, and/or between egg-layings in order to understand the significance of this. Perhaps these slugs are effectively monogamous, at least as males, each in-dividual mating once upon attaining adulthood and losing its penis in the process, with occasional individuals surviving long enough to regenerate the penis and copulate as males a second time? Its amazing how little we know about such common and conspicuous animals.

SIMULTANEOUSLY RECIPROCAL COPULATION

STYLOMMATOPHORANS

Both Hyman (1967) and Franc (1968) made the inter-esting generalization that basommatophorans have unilateral copulation associated with a short, simple courtship per-formed by the individual that will act as the male, whereas stylommatophorans have simultaneously reciprocal copula-tion preceded by lengthy, elaborate, and often bizarre court-ship behavior. The usual explanation of this phenomenon has been mechanistic; i.e. that the behavior serves to facilitate coordination between the partners to allow simultaneous reciprocal intromission, and most of the experimental work has focused on that aspect of the behavior (i.e. *Helix*, Jep-pesen, 1976; Lind, 1976; Chung, 1986; Adamo and Chase, 1988; Giusti and Andreini, 1988). However, because many opisthobranchs, particularly nudibranchs, have simultaneous reciprocal copulation without lengthy or notably peculiar courtship behavior (Hadfield and Switzer-Dunlap, 1984; Leonard, unpub. data; see also aeolids below), it is difficult to argue that simultaneous reciprocal copulation must be ac-companied in evolution by such bizarre mechanisms as the love-dart of *Helix*, the ingestion of caudal mucous globules, the aerial performance of *Limax maximus* (L.), etc. (see Hyman, 1967; Franc, 1968; Tompa, 1980). An obvious func-tional or adaptive explanation is that these elaborate court-ship behaviors have evolved through sexual conflict.

Specifically, the Hermaphrodite's Dilemma model pre-dicts that they all serve to prevent "cheating" on the recipro-cal mating system, which should take (according to the gamete-trading model) the form of individuals attempting to act as females, receiving sperm, without offering any of their own. Both Meisenheimer (1907) and Lind (1976) reported that in *Helix*, that an individual (A) that inserts its penis into the vagina of its partner (B) will immediately withdraw its penis unless B simultaneously inserts its (B's) penis into A's vagina (but see Chung, 1987). This is consistent with the idea that courtship serves to prevent an individual from acting only as a male. Similar reluctance to act as a male before the part-ner does should be seen in other species with elaborate court-ship and simultaneous reciprocal copulation. The courtship therefore, should enforce reciprocity, specifically by prevent-ing individuals from acting only as females. An egg-trading model, based on Bateman's principle would predict the op-posite; that is the courtship serves to enforce reciprocity by preventing individuals from "cheating" by acting only in the male role. One would predict therefore that in these elaborate courtships there should be evidence that individuals are 1) coy as females, refusing to allow intromission until they have an opportunity to act as a male; and 2) eager as males,

competing with each other for the first intromission. Charnov (1979) suggested that such "complicated precopulatory displays" should serve (under Bateman's principle) to induce the partner to use the sperm received to fertilize eggs. These hypotheses should be testable by experimental and comparative studies of common species of stylommatophorans.

AEOLIDS

While Lind (1976) reported that unilateral copulations were rare in *Helix*, Rutowski (1983) found that 49% of all copulations in *Hermissenda* were non-reciprocal. Rutowski (1983) discussed this phenomenon in terms of sexual conflict and Charnov's (1979) prediction, considering the possibility that the failure of one individual to intromit after everting its penis was the result of an effort by its partner either to deflect the penis of its partner or to give sperm quickly without receiving any. That is, that one individual was attempting to "cheat" by mating only in the male role. He concluded that this was unlikely because many of the "missed individuals" were sperm-depleted and would have benefited from receiving sperm.

If, as the gamete-trading model (Leonard and Lukowiak, 1984, 1985) predicts, the female sexual role is preferred, the "cheater" in a unilateral copulation would be the individual receiving but not giving sperm. These unilateral intromissions in *Hermissenda* could represent "cheating" by "deliberately" missing the target. However, since Rutowski (1983) reported that sperm was ejaculated into the water as a result of these "missed" intromissions this seems improbable. It seems very unlikely that emission of sperm into the water would be more adaptive than transferring it to a partner, especially because Rutowski's (1985) observation that *Hermissenda* ingest any sperm left on the gonopore suggests that the caloric content of sperm is not trivial. I agree, therefore, with Rutowski's conclusion that the high frequency (49%) of copulations in which only one individual achieves intromission is probably a consequence of whatever factors have selected for extremely rapid copulation in this species. However, on the assumption that the female sexual role is preferred in *Hermissenda*, I suggest that cheating was represented in Rutowski's observations by those copulations (5% of the total) which were unilateral because only one individual everted its penis, because in these cases individuals received sperm without giving any in return (or wasting any). A more detailed study of the mating behavior of *Hermissenda* as a function of the sperm stores of the interacting individuals might serve to test this possibility. In particular, Rutowski's observation that most of the "missed individuals" in only semi-successful reciprocal copulation attempts were sperm-depleted is intriguing. One would like to know if sperm-depleted animals behave differently during mating encounters, and/or if their depleted status is detectable by partners who then treat them differently. One would expect that, if there

is any difference, sperm-depleted individuals ought to be both more willing to receive sperm, and more attractive as female partners, than individuals with full sperm stores.

Observations from another aeolid, *Aeolidia papillosa* Bergh, are also suggestive of cheating in a mating system based on reciprocation. The sexual behavior of *Aeolidia* is very similar to that of *Hermissenda* (Longley and Longley, 1982, 1984); encounters are very brief and usually simultaneously reciprocal. However, in *Aeolidia* there is no copulation, sperm packets are deposited on the partner's gonopore (Longley and Longley, 1984). The Longleys observed one individual which copulated repeatedly (over a period of days) without producing sperm packets. These authors also reported that the quantity of sperm transferred in a copulation was determined by both 1) the duration of the copulation, which is correlated with the size of the smaller partner, and 2) the rate of sperm transfer, which is related to the number of autosperm remaining in the ampulla. This raises the possibility that *Aeolidia* could engage in what Trivers (1971) termed "subtle cheating." That is, an *Aeolidia* could cheat by engaging in a reciprocal mating when it has relatively few autosperms available, and thereby receive more sperm than it gives to its partner. Beeman (1970a) also observed instances in which only one member of a pair of reciprocally copulating *Phyllaplysia taylori* Dall transferred sperm to its partner, since the other's ampulla was empty.

Observations on many species with simultaneous reciprocal copulation mention that unilateral copulations sometimes occur (e.g. *Helix*: Herzberg and Herzberg, 1962; Lind, 1976; opisthobranchs: Hadfield and Switzer-Dunlap, 1984; including *Aeolidia papillosa*: Longley and Longley, 1984; *Hermissenda crassicornis*: Longley and Longley, 1982; Rutowski, 1983; *Melilbe*: Agersborg, 1922) which could be considered "cheating." In summary, there is some evidence that "cheating" can occur occasionally in species with simultaneous reciprocal copulation, in the form of unilateral copulations and/or "subtle cheating." However, from the available evidence one cannot say with confidence that "cheating" does or does not occur in these species. The evidence does suggest that studies directed to the analysis of sexual conflict in this group would be very rewarding.

DISCUSSION

The review and analysis presented here suggest that 1) gastropods offer a broad array of reproductive phenomena that require explanation in terms of mating systems theory; 2) Hermaphrodite's Dilemma model makes nontrivial predictions about the mating systems of hermaphroditic gastropods that may serve to test the model; 3) for many euthyneuran gastropods the egg-trading and gamete-trading models make opposing predictions, making this group a useful means of

distinguishing between the two models. While experimental studies can be used to determine the preferred sexual role for a given species (Leonard and Lukowiak, 1991), comparative studies can also be useful here. Review of the range of mating systems found in simultaneously hermaphroditic serranid fishes (Leonard, unpub. data) provides strong support for the existence of sexual conflict since it provides confirmation of the hypothesis that the male sexual role is preferred in these simultaneous hermaphrodites, as assumed by Fischer (1980, 1984) and predicted by Charnov (1979). The evidence for this is twofold. First, in all species studied, "cheating," on a reciprocal mating system, whether as streaking or as extra-pair spawning in the monogamous *Serranus tigrinus* (Bloch) (Pressley, 1981), is a male behavior; cheaters "cheat" in order to fertilize someone else's eggs, not to get their own eggs fertilized. Second, where mates become a defensible resource, large, dominant individuals become male (e.g. *S. fasciatus* (Jenyns) and *S. baldwini* (Evermann and Marsh) (Petersen, 1990). In serranids, then, the harem-based mating systems are exceptions that prove the egg-trading rule. These simultaneously hermaphroditic fish provide strong evidence that sexual conflict both exists and is important in shaping mating systems. However, both the gamete-trading and the egg-trading models predict (indeed the gamete-trading model assumes) that serranids prefer the male role so that the serranids do not allow us to distinguish between the egg-trading and gamete-trading models (contrary to Fischer, 1987). The gastropods therefore, offer an exciting opportunity not only to test the assumption that sexual conflict exists but also to distinguish between models based on different assumptions about the source of sexual conflict. The variety of reproductive behavior and physiology found within the gastropods should allow us to identify species that can be used to test hypotheses about the relative importance of energy investment, mating time and control of fertilization in sexual conflict.

In this paper I have attempted to demonstrate that analysis in terms of sexual conflict makes specific predictions about gastropod mating systems that may allow us to elucidate the adaptive significance of many bizarre phenomena in gastropod reproductive biology. The available literature on gastropod sexual behavior suggests a number of interesting test cases for the Hermaphrodite's Dilemma model, but does not, in itself, provide sufficient data to test the model. The chief difficulty interpreting the available information on gastropod reproduction in terms of sexual conflict or sexual selection is that one can seldom determine from the available descriptions which types of behavior represent the rule and which the exceptions. Where the initial studies were not informed by mating systems theory or selection thinking, crucial information is apt to be lacking, even when there have been numerous detailed studies of the behavior, as in *Helix* (Leonard, unpub. data). Mating systems theory

has a lot to offer to the study of euthyneuran gastropods and euthyneuran gastropods have a lot to offer to the study of mating systems theory.

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